

THE KARYOTYPE OF THE EURASIAN FLYING SQUIRREL, *PTEROMYS VOLANS* (L.), WITH A CONSIDERATION OF KARYOTYPIC AND OTHER DISTINCTIONS IN *GLAUCOMYS* SPP. (RODENTIA: SCIURIDAE)

V. R. Rausch and R. L. Rausch

Abstract.—The karyotype of *Pteromys volans* (L.) ($2n = 38$; $FN = 73$) is described, based on material from Hokkaido and northeastern Siberia, and compared with those of *Glaucomys volans* (L.) ($2n = 48$; $FN = 80$) and *Glaucomys sabrinus* (Shaw) ($2n = 48$; $FN = 78$) from North America. Although the similarities of the fundamental numbers are suggestive of karyotypic evolution of the Robertsonian type, the fossil record of these flying squirrels is at present fragmentary, and no conclusion is drawn as to their affinities. Definite differences were observed between the karyotypes of *G. volans* and *G. sabrinus*, which had been described as identical. In combination with karyotypic differences, other characteristics of the two North American species indicate both a divergence earlier and an age greater than have been considered on the basis of paleontologic evidence. Karyograms of the three species of flying squirrels are included.

In the course of investigations concerning northern mammals, we studied chromosomal preparations from two specimens of the Eurasian flying squirrel, *Pteromys volans* (L.), from Hokkaido and northeastern Siberia. Chromosomes of the two species of flying squirrels of the Nearctic genus *Glaucomys* were compared. The purpose of the present report is to define the karyotype of *P. volans* and to describe some previously unrecognized differences in the karyotypes of the two Nearctic species. Other distinguishing characteristics of *Glaucomys* spp. also are briefly discussed.

Materials and Methods

Two male specimens of *P. volans* were utilized. The first, *P. volans orii* Kuroda, was provided in 1967 by Dr. H. Abe, who captured the animal at Koshimizu, Abashiri, Hokkaido Island (ca. $43^{\circ}58'N$, $144^{\circ}30'E$). Cells from bone marrow and from one testis were fixed and stained in acetic orcein, following standard methods for mammalian karyology. The second, *P. volans* cf. *incanus* Miller, was trapped by us in August 1979 along the upper Kolyma River, Magadansk Oblast', near the settlement of Sibik-Tiellakh (ca. $62^{\circ}N$, $149^{\circ}30'E$). Cells from marrow (femur) were prepared in the field and processed with Giemsa blood stain (Seabright 1972). In both cases, cells were treated with colchicine.

Preparations were made by the same methods for Nearctic flying squirrels, as follows: *Glaucomys sabrinus yukonensis* (Osgood), two males collected at Anchorage and near Fairbanks, Alaska, in October 1966 and April 1969, respectively; one male *G. sabrinus bangsi* (Rhoads), captured on Powwatka Ridge, Wallowa Mountains, Oregon (ca. $45^{\circ}40'N$, $117^{\circ}27'W$), in December 1980; and one male *G. volans querceti* (Bangs), collected in the vicinity of Tampa, Florida, in early 1980.

After chromosomes (in metaphase) were counted, representative cells were photographed on high-contrast film, and the component chromosomes in five cells from each animal were measured (excepting the squirrels from the upper Kolyma River and from Anchorage, in which only contracted chromosomes were observed in the preparations). Chromosomes exhibiting Giemsa-banding were segregated according to size and banding-pattern with use of photographs and light microscopy. The identification of the X-chromosome was based on measurements and pattern of banding. The Y-chromosome in *Glaucomys* spp. was selected subjectively, since the small submetacentric chromosomes in these animals, of which the Y is one, appeared to be similar in both size and banding. The terminology concerning the location of the centromere on individual chromosomes follows Levan *et al.* (1964). The number of major chromosomal arms (fundamental number, or FN) was determined according to the procedure of Matthey (1945). The chromosomal components of 30 to 61 cells from each of the animals were counted, excepting those from the upper Kolyma River and Anchorage for which only 18 and 15 cells, respectively, were counted.

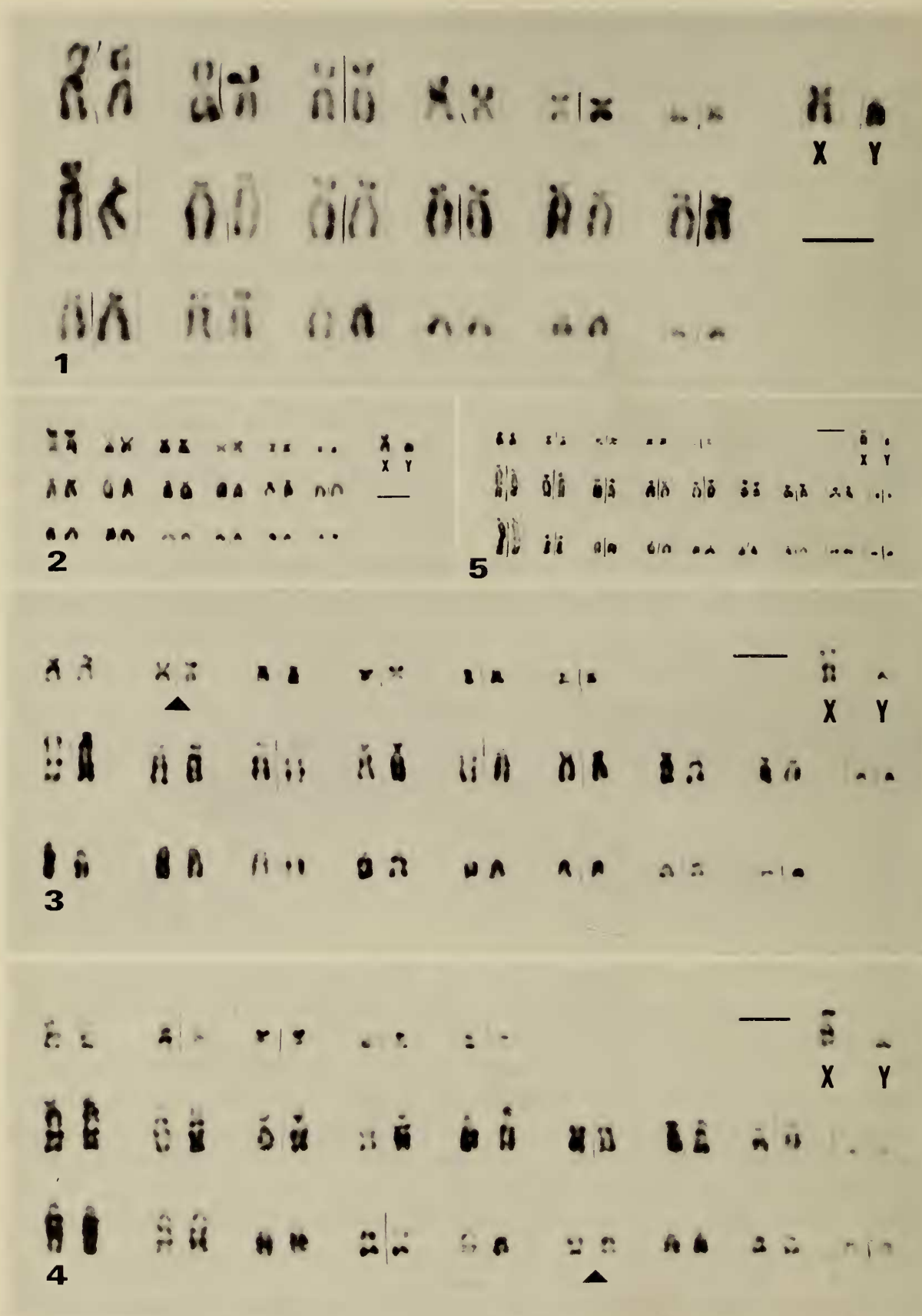
Results

I. Pteromys volans ($2n = 38$, $n = 19$).—The diploid complement was made up of 12 metacentric autosomes (arm-ratios ranged from 1.03 to 1.7), 22 submetacentric-subtelocentric and 2 acrocentric autosomes (arm-ratios from 2.4 to 6.3), the submetacentric X-chromosome (arm-ratio from 1.6 to 1.8), and the acrocentric Y-chromosome (arm-ratio from 4.2 to 7.3). In 61 cells (53 mitotic and 8 meiotic) examined, 49 contained 38 chromosomes and 7 contained 19 bivalent elements. A karyogram from the male *P. volans* from Hokkaido is shown in Fig. 1.

The set of chromosomes (in all of the 18 cells examined) from the animal collected in northeastern Siberia was morphologically like that of *P. volans* from Hokkaido, consisting of 6 pairs of metacentric and 12 pairs of submetacentric-acrocentric autosomes, a submetacentric X, and an acrocentric Y-chromosome, as shown in Fig. 2.

The number of major autosomal arms was 70 in both animals. Two autosomes with thin and lightly stained short arms were considered to be acrocentric. The FN (autosomes + X and Y) was 73 for *P. volans*.

II. Glaucomys spp. ($2n = 48$).—Karyograms from *G. volans* (Florida) and from *G. sabrinus* (Oregon and Alaska) are shown in Figs. 3–5. Thirty bi-armed (metacentric-subtelocentric) chromosomes (with arm-ratios ranging from 1.03 to 8.8) and 16 acrocentric chromosomes (with centromeres in the terminal region; arm-ratios ranged from 4.5 to 13.8) constituted the autosomal set in *G. volans*. In *G. sabrinus*, from both localities, the autosomes included 28 metacentric-subtelocentric (arm-ratios ranging from 1.07 to 8.6) and 18 acrocentric (arm-ratios from 4.3 to 14.5) elements. The sex-chromosomes of the two species were similar morphologically and in pattern of banding: X submetacentric, of medium size (ranges of arm-ratios were 1.5 to 2.03 for *G. volans*, and 1.9 to 2.9 for *G. sabrinus*), and Y submetacentric of small size (ranges of arm-ratios were 2.1 to 3.2 for *G. volans*, and 2.0 to 3.3 for *G. sabrinus*). The patterns of bands indicated that these two species have some equivalent, or homologous, chromosomes. However, significant morphologic differences also were evident.



Figs. 1-5. Karyograms of *Pteromys volans* ($2n = 38$) and *Glaucomys* spp. ($2n = 48$). 1, *P. volans*, male, from Hokkaido Island; Orcein stain. 2, *P. volans*, male, from the Magadansk Oblast; Giemsa blood stain. 3, *G. volans* with Giemsa-bands, male, from Florida. Arrow indicates metacentric elements not present in *G. sabrinus*. 4, *G. sabrinus* with Giemsa-bands, male, from Oregon. Arrow indicates acrocentric elements not present in *G. volans*. 5, *G. sabrinus*, male, from Alaska; Orcein stain. Scale-lines have value of $5 \mu\text{m}$.

Discussion

The gliding squirrels allocated to the genera *Pteromys* G. Cuvier, 1800, and *Glaucmys* Thomas, 1908, have had rather complex taxonomic histories and, as indicated by recent reviews (cf. Mein 1970, Black 1972), their origins and affinities are obscure. The grounds for acceptance of the genus *Pteromys* instead of *Sciuropterus* F. Cuvier, 1825, for the flying squirrel in northern Eurasia have been discussed by Miller (1914) and by Ellerman and Morrison-Scott (1951), among others, but Simpson (1945) considered the latter to be probably the valid generic designation. In addition to the widely occurring *P. volans*, the genus includes a second species, *P. momonga* Temminck, 1846, which occurs on the Japanese Islands of Honshu, Kyushu, and Hondo. According to Ellerman and Morrison-Scott (1951), its cranial differences are so marked that it cannot be considered a race of *P. volans*.

In his revision of the genera and subgenera of the *Sciuropterus*-group of flying squirrels, Thomas (1908) recognized four subgenera in *Sciuropterus*, mainly on the basis of dental characters. These included *Sciuropterus*, with *S. (Sciuropterus) russicus* Tiedemann, 1808 (= *Sciurus volans* Linnaeus, 1758) as type, and *Glaucmys*, which was erected for the Nearctic flying squirrels, with *S. (Glaucmys) volans* (= *Mus volans* Linnaeus, 1758) as type. *Glaucmys* was elevated to generic rank by Howell (1915), on grounds not stated, but he later (1918) defined cranial and dental characters that distinguish *Glaucmys* from *Pteromys*. These distinctions were confirmed by Ognev (1940), who also pointed out the marked differences in the structure of the os penis in *P. volans* and *G. volans*. Recently, from the study of both fossil and living flying squirrels, Mein (1970) placed *Pteromys* and *Glaucmys* in different generic groupings on the basis of dental characters.

The fossil record provides no clear indication of the origin of *Pteromys volans*. However, the comparison of serum proteins by means of double immunodiffusion by Zholnerovskaia *et al.* (1980) suggested that *Pteromys* has its closest affinities with *Sciurus* and *Tamias*, rather than with terrestrial sciurids. In North America, *Glaucmys* is known from the middle to late Irvingtonian. The stratigraphic range of *Glaucmys volans* extends from the late Irvingtonian, whereas remains of the northern *G. sabrinus* are known only from deposits of late Würm age (Kurtén and Anderson 1980). Thenius (1972) considered that *Glaucmys* appears to have arisen from terrestrial sciurids, which had their center of radiation in North America.

The diploid number of 38 chromosomes, as reported by Tsuchiya (1979) and determined by us, alone distinguishes the karyotype of *Pteromys volans* from those of *Glaucmys* spp. ($2n = 48$) (Nadler and Sutton 1967, Schindler *et al.* 1973). In the former, 35 chromosomes were metacentric-subtelocentric, and only 3 (two autosomes and the Y-chromosome) were acrocentric. The relatively large, acrocentric Y of *P. volans* is markedly different from the male sex-chromosomes of *Glaucmys* spp. That the fundamental numbers in these squirrels are rather similar (73 in *P. volans*; 78 in *G. sabrinus*; and 80 in *G. volans*) suggests that karyotypic evolution involving chromosomal rearrangements of Robertsonian type might have occurred. However, no significance is attributed to the apparent similarities when nothing is known concerning the further relationships of the Eurasian and American species.

The karyotype of a female specimen of *P. momonga* has been published by Tsuchiya (1979, fig. 7). It appears to be quite similar to that of *P. volans*, but the available details do not permit an extensive comparison. The presence of boreal forest far to the south in the Japanese Islands during the glacial maximum of Würm time would seem to have favored the southward dispersal of *Pteromys volans* (cf. Kotani 1969).

With reference to the karyotypes of *Glaucomys* spp., the published information is discrepant. That *G. volans* and *G. sabrinus* are karyotypically identical has been generally accepted. However, for both, Schindler *et al.* (1973) considered the number of bi-armed (metacentric-subtelocentric) autosomes to be two more than did Nadler and Sutton (1967). Hsu and Benirschke (1973) concurred with Schindler *et al.* The karyotype defined by us for *G. sabrinus yukonensis* (Alaska) agreed more closely with that shown and discussed by Nadler and Sutton (1967), who studied preparations from *G. sabrinus lascivus* (Bangs) (California), than with the results of Schindler *et al.* (1973) for *G. sabrinus* from New Hampshire (an area where this species is marginally sympatric with *G. volans*). Accordingly, we examined new material from *G. sabrinus* as well as *G. volans*, from geographic regions far removed from areas of parapatry or sympatry (Oregon and Florida). The identities of the animals studied were confirmed from the distinctive characteristics of the os penis, in addition to other criteria.

Although the respective karyotypes of these flying squirrels appeared superficially to be much alike, they exhibited distinct differences, principally in the presence in *G. volans* of two small metacentric autosomes that did not occur in *G. sabrinus*, and in *G. sabrinus* of two small acrocentric autosomes not observed in *G. volans*. As well, the total lengths of individual chromosomes differed between the two species, including those in some presumed to be homologous; the relative length of the female haploid complement (autosomes + X) was recorded as 65 μm in *G. volans* and 86 μm in *G. sabrinus*. Morphologically, the sex-chromosomes were similar.

Of the chromosomes of *G. volans*, the two small metacentric autosomes (see Fig. 3, arrow) were the most nearly metacentric, *sensu stricto*, with an arm-ratio ranging from 1.03 to 1.05. However, these and the two small acrocentric elements in *G. sabrinus* (see Fig. 4, arrow) were similar in total length; their value relative to the lengths of the respective haploid complements was the same (3.5%) in both species. The appearance of Giemsa-bands in these chromosomes suggests that they may be homologues, and that the small metacentric pair in *G. volans* arose as a result of a pericentric inversion involving the small acrocentric pair in *G. sabrinus* (or perhaps vice versa). The disparate total lengths of the respective complements further suggest quantitative differences in nuclear DNA, which were not defined by our methods.

Our findings indicate that the two species of *Glaucomys* are karyotypically distinct, and they are in contrast with the conclusions of others concerning these flying squirrels. The karyogram from *G. volans* from Florida (Fig. 3) appears to be identical with those shown by Schindler *et al.* (1973) as representative of both *G. volans* and *G. sabrinus* in New Hampshire, where the two species are sympatric.

The two species of *Glaucomys* are distinguished additionally by major differences in the form of the os penis, as is also *Pteromys volans*. Since detailed

Table 1.—Helminths of *Glaucomys volans* and *G. sabrinus*.

Species of helminth	<i>G. volans</i> Midwest (n = 22) no. infected	<i>G. sabrinus</i>	
		Midwest (n = 5) no. infected	Oregon (n = 26) no. infected
Nematoda:			
<i>Capillaria americana</i> Read, 1949	7	—	—
<i>Syphabulea thompsoni</i> (Price, 1928)	1	5	—
<i>Syphabulea</i> sp.*	—	—	17
<i>Lemuricola sciuri</i> (Cameron, 1932)	13	—	—
<i>Citellinema bifurcatum</i> Hall, 1916	2	2	7
Cestoda:			
<i>Andrya sciuri</i> Rausch, 1947	—	2	4
<i>Monoecocestus thomasi</i> Rausch and Maser, 1977	—	—	18
<i>Catenotaenia</i> sp.	—	3	—
<i>Hymenandrya</i> sp.	—	—	3

* Description in preparation by J.-P. Hugot, Muséum National d'Histoire Naturelle, Paris.

descriptions of these structures have been published, it suffices here to point out their diversity in the three species. The os penis of *P. volans* is small (ca. 4 mm long in our material) and consists of a slender, pointed bone with a well developed barb at the proximal end (cf. Ognev 1940, fig. 153). That of *G. volans*, first described by Pocock (1923), is long (ca. 14 mm in specimens from Florida) and very slender, whereas that of *G. sabrinus* is shorter (ca. 6.5 mm in our material), broader, and flattened (see Burt 1960, plate IV). Each differs markedly from the others, and we were unable to discern any fundamental similarities unless, perhaps, the barb near the distal end of the os penis of *G. sabrinus* is homologous with the basal barb in that of *P. volans*.

Certain differences in the helminth faunas of the two species of *Glaucomys* provide a further indication of dissimilarity. Of the nine species of helminths recorded by us from flying squirrels in North America (Table 1), six occur also in sciurids of other species (Rausch and Tiner 1948, Davidson 1976, McGee 1980). Host-specific cestodes of three species, *Andrya sciuri*, *Monoecocestus thomasi*, and *Hymenandrya* sp., are known only from *Glaucomys sabrinus*. The assemblages involving these cestodes would seem to have arisen independently through coevolution of helminth and host (Rausch 1981), indicating comparatively early divergence of the two species of *Glaucomys*. These cestodes are Nearctic species, with no congeners known from *Pteromys volans* or other sciurids in Eurasia. The only helminth known from *P. volans* is *Citellina petrovi* Shul'ts, 1930, which is host-specific and has been recorded from European Russia, Japan, and Chukotka (Hugot 1980). Some of the characteristic ectoparasites of *Pteromys volans* and *Glaucomys* spp. are congeneric (Acarina and Mallophaga), but no species is shared. Consequently, these arthropods do not appear to provide any useful indications of the relationships of their hosts.

Various hypotheses have been proposed to account for the essential allopatry of the Nearctic flying squirrels, but the geographic ranges of these mammals seem simply to reflect differences in specific ecologic requirements. The two species occupy disjunct ranges over the greater part of North America where they occur,

relative to the distribution of coniferous and deciduous forest. In the east, where their ranges are parapatric to sympatric, they appear as well to be segregated ecologically. As noted by Guilday (1962), *G. sabrinus* has a relict distribution in the Appalachian Mountains, where it occurs at elevations above ca. 1000 m as a consequence of climatic change (warming) during post-glacial time.

That the characteristic habitats of the two species of *Glaucomys* have a fundamental relationship to their different dietary requirements is evident. *Glaucomys volans* utilizes buds, fruits, and insects during spring and summer, but later feeds mainly on acorns and other nuts and seeds, some of which are stored in large quantities and consumed during winter (cf. Muul 1968). *Glaucomys sabrinus* depends mainly on hypogeous fungi during the warmer months, and utilizes epiphytic lichens (*Usnea* and *Alectoria*) during winter (McKeever 1960, Maser *et al.* 1978, Maser pers. comm.). The diet of *Pteromys volans* differs from these in that it feeds on sprouts or buds of *Betula* and *Acer* and on male flowers of conifers in summer, and on catkins or buds of *Betula* and *Alnus* in winter (Ognev 1940, Tavrovskii *et al.* 1971).

Suggestions have been made to account for the pattern of distribution of *Glaucomys sabrinus* on grounds other than ecologic requirements. Muul (1968) considered that the southward spread of *G. sabrinus* is prevented by competitive interaction with *G. volans*, inasmuch as the latter breeds earlier seasonally and therefore would already occupy the limited number of tree-cavities available. However, as reported by Cowan (1936), and observed by us in northern Wisconsin, *G. sabrinus* commonly utilizes outside nests constructed mainly of twigs.

Weigl (1975) observed in captive animals that infection by a nematode of the genus *Strongyloides* was tolerated by *G. volans*, but was associated with high mortality in *G. sabrinus*. He considered that differential pathogenicity of this nematode might account in part for the segregation of the two species of *Glaucomys* where they are sympatric. Barbehenn (1978) suggested that this might constitute a mechanism by which the larger *G. sabrinus* would be excluded from habitat otherwise suitable for *G. volans*. However, *Strongyloides robustus* Chandler, 1942 exhibits little host-specificity, occurring in sciurids of various species (Rausch and Tiner 1948, McGee 1980). Davidson (1976) considered it to be the most pathogenic of the more common helminths in squirrels, and reported that infections involving more than 150 individuals often caused severe enteritis in gray squirrels, *Sciurus carolinensis* Gmelin. It might be expected that transmission of this nematode would be enhanced by conditions of captivity, and that differences in feeding habits or other behavior could account for more massive infections in *G. sabrinus*. That Weigl did not find northern flying squirrels naturally infected by *Strongyloides* appears to be compatible with the results of other surveys of helminths in this sciurid.

Altogether, the differences between the two flying squirrels of the genus *Glaucomys* seem to indicate earlier divergence and greater age of these species than has been considered on the basis of paleontologic evidence. The origins and affinities of *Glaucomys* spp. and of *Pteromys volans* may be established if the earlier fossil record of these sciurids can be traced.

Acknowledgments

Specimens of flying squirrels were kindly provided by H. Abe, Faculty of Agriculture, Hokkaido University, Sapporo; Ms. E. L. Bull, Pacific Northwest

Range and Habitat Laboratory, U.S. Department of Agriculture, La Grande, Oregon; R. Anderson, Wallowa Valley Ranger District, U.S. Department of Agriculture, Joseph, Oregon; and I. L. Duncan, Center for Disease Control, Atlanta. Field work in the Soviet Union was carried out under the U.S.A./U.S.S.R. Environmental Protection Treaty, Area V, Subproject A-3. In the U.S.S.R., V. L. Kontrimavichus, D. I. Berman, and Ms. A. N. Leirikh, Institute of Biological Problems of the North, Academy of Sciences of the U.S.S.R., Magadan, kindly provided support and assistance. We express sincere thanks for these contributions.

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Burke Memorial Washington State Museum, DB-10, and Division of Animal Medicine, SB-42, University of Washington, Seattle, Washington 98195.